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Effects of Fishing on the Ecosystem Structure of Coral Reefs

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Abstract: *Overfishing is considered one of the three most significant threats to coral reef ecosystems. Exponentially increasing human populations in the tropics have placed enormous demands upon reefs as a food source. At high intensities, termed ecosystem or Malthusian overfishing, fishing causes major direct and indirect effects on the community structure of fishes and other organisms. It reduces species diversity and leads to local extinctions not only of target species but also of other species not fished directly. Conceivably it could also lead to global extinctions. Loss of keystone species, such as predators of echinoderms, through fishing, can lead to major effects on reef processes, such as accretion of calcium carbonate. Ultimately, sustained heavy fishing may lead to loss of entire functional groups of species, resulting in impairment of the potentially important ecosystem functions provided by those groups. Overfishing has been shown to interact with other agents of disturbance to reduce the ability of reefs to recover from natural occurrences such as hurricanes. Effective management of fishing will require a deeper understanding of the effects of exploitation than we now possess. Research initiatives are underway to examine the responses of fish populations to fishing, generally responses to protection from fishing. There is, however, an urgent need to look beyond fish communities and to consider the entire reef ecosystem. Studies that integrate population and community biology with ecosystem processes will provide a much better understanding of the effects of biodiversity loss on reef function and will improve our ability to manage these complex systems.*

Efecto de la pesca sobre la estructura ecosistémica de los arrecifes de coral

Resumen: *La sobrepesca es considerada como una de las tres amenazas más significativas para los arrecifes de coral. En los trópicos, las poblaciones humanas en incremento exponencial han impuesto demandas enormes sobre los arrecifes como fuentes de alimentos. A intensidades de pesca altas, denominadas sobrepesca ecosistémica o Maltusiana, la pesca causa importantes efectos directos e indirectos en la estructura de la comunidad de peces y otros organismos. La sobrepesca reduce la diversidad de especies y lleva a la extinción local tanto de las especies pescadas como de otras especies no pescadas en forma directa. En forma concebible puede también llevar a extinciones globales. La pérdida de especies clave por medio de la pesca, tales como predadores de equinodermos, puede tener efectos importantes sobre los procesos biológicos del arrecife, tales como la acumulación de carbonato de calcio. En última instancia, la pesca intensiva sostenida puede llevar a la pérdida de grupos funcionales de especies enteras, lo que resulta en la pérdida de las funciones ecosistémicas potencialmente importantes provistas por estas especies. Se ha demostrado que la sobrepesca interactúa con otros agentes perturbadores para reducir la habilidad de los arrecifes para recuperarse de fenómenos naturales como los huracanes. El manejo pesquero efectivo requerirá de un entendimiento más profundo de los efectos de la explotación. Se están llevando a cabo iniciativas de investigación para examinar las respuestas de las poblaciones de peces a la pesca, se trata generalmente de estudios sobre la respuesta de las poblaciones a la protección de la pesca. Existe sin embargo, una necesidad urgente de mirar más allá de las comunidades de peces y considerar a la totalidad del ecosistema. Los estudios que integran la biología de poblaciones y comunidades con los procesos ecosistémicos, proveerán de un mejor entendimiento de los efectos de la pérdida de la biodiversidad sobre las funciones de los arrecifes y mejorarán nuestra habilidad para manejar estos sistemas complejos.*

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Introduction

At a recent meeting on the global status of coral reefs, overfishing was deemed one of the three most serious threats to reefs (Roberts 1993). In November 1993 a workshop was convened by SCOPE (Scientific Committee on Problems of the Environment) to examine the effects of biodiversity loss on the function of the coral reef ecosystem (Done et al. in press). Fishing was also a recurrent theme at this meeting. I examine fishing as an agent of biodiversity loss on coral reefs and seek to determine the implications of species loss for reef ecosystem processes.

The effects of fishing on coral reefs have often been overlooked because most reefs have been exploited for a long time, especially in places scientists tend to study. Recent increases in fishing intensity, however, to levels termed ecosystem or Malthusian overfishing (Pauly 1988; Russ 1991), have led to the effects of fishing becoming more widely recognized and studied.

A review of the data on reef fishing reveals the following points: (1) it can lead to major direct and indirect shifts in community structure, both of fishes and of reef communities as a whole (Bohnsack 1982; Munro & Williams 1985; Lock 1986; Koslow et al. 1988; Russ & Alcala 1989; Russ 1991; Medley et al. 1993; Jennings & Lock in press); (2) it reduces species diversity on reefs (Clark et al. 1989; Roberts & Polunin 1991; Polunin & Roberts 1993; Roberts 1995; Bohnsack in press); (3) it can result in loss of keystone species, which in turn can lead to major effects on reef processes (Munro et al. 1987; McClanahan & Muthiga 1988; Hughes 1994; McClanahan & Mutere 1994); and (4) it may lead to loss of entire functional groups of species, resulting in impairment of potentially important ecosystem processes facilitated by those groups (Messiha-Hanna & Ormond 1982; Hay 1984; Hay & Taylor 1985; Hughes 1993).

My arguments are based on data derived primarily from comparative studies, although some supporting experimental work has been done. This reflects fairly accurately the state of research on the effects of fishing and highlights the need for more focused and manipulative studies, especially ones that look beyond fishes alone to other reef groups and processes.

Undoubtedly there are infinite ways of assembling a reef community. The seas are full of variations on the theme, with differences present at scales from meters to oceans. The huge variability in species composition and trophic structure, especially at geographic scales, has not noticeably impaired the function of reefs (Harmelin-Vivien 1989; Roberts 1991; Williams 1991; Roberts et al. 1992) although the possibility that fishing might have shaped some of these differences has rarely been considered. It can be argued that reefs can afford to lose a few species here and there, and with some justification. But I believe we are no longer tinkering with the mechanism,

adjusting a surgeonfish population here, removing a grouper species there; rather, we are in danger of harvesting reefs into oblivion.

Effects of Fishing on Fish Communities

Several recent papers have reviewed the effects of fishing on coral-reef fish communities (Munro & Williams, 1985; Roberts & Polunin 1991; Russ 1991; Medley et al. 1993; Jennings & Lock in press). The effects depend on the intensity of fishing, but even at low intensities they can be marked. Briefly, fishing leads first to reduced abundance or loss of predatory species, especially piscivores. Such losses lead to a concomitant reduction in species diversity, which is probably not compensated by responses of prey populations (Polunin et al. in press). Mostly, loss of predators is a local effect, but widespread and intensifying fishing has led to the possibility of global extinction for species especially vulnerable to capture (Sadovy 1993). But because many reef processes operate at local scales, it is a local loss of species that is important to those processes; when I refer to loss of species, unless otherwise indicated, I mean local losses.

Loss of predators has not led to obvious increases in abundance of prey species, perhaps because other opportunistic predators switch feeding preferences or perhaps because this effect is masked by population fluctuations due to recruitment variability (Bohnsack 1982; Russ 1991). There is substantial evidence, however, for shifts in the relative abundance of species, from data on catch trends, comparisons across fishing gradients, and studies of responses of communities to protection from fishing (Appeldoorn et al. 1992; Roberts & Polunin 1991; Butler et al. 1993; Bohnsack et al. 1994). Where fishing is of sufficient intensity to cause such shifts it has been termed "ecosystem overfishing" (Pauly 1988).

Fishing may also have marked effects on the size composition and life-history characteristics of species and on the genetic structure of stocks, but these effects will not be considered here. Rather I focus on changes in the abundance of fish species and other organisms and their potential influence on reef processes.

High-intensity fishing, termed "Malthusian overfishing," constitutes the most extreme manifestation of human exploitation of reef organisms. Throughout large areas of the developing world human populations have been expanding, leading to rapidly increasing pressure on limited resources. On reefs this has resulted in fishing levels and methods that cause wholesale resource destruction (Pauly 1988; McManus in press, unpublished data). Fine-mesh nets, weighted scare lines, poisons, and dynamite are all employed in an overfishing spiral in which more and more fishers chase fewer and fewer fish (Alcala & Gomez 1987; Gomez et al. 1987). In places such as the Philippines, Haiti, and Jamaica, fish population densities

have plummeted, and adults of edible species have been virtually eliminated, leaving reef habitat severely damaged and populations probably unable to replace themselves (Sadovy 1989; Russ 1991; Appeldoorn & Meyers 1993).

Effects of Fishing on Reef Processes

Loss of Keystone Species

Since the idea of keystone species was introduced by Paine (1966), the concept has proven very useful in linking population and community processes. Many fishes play a keystone role in the reef ecosystem, and they are undoubtedly affected by fishing. The best-known and probably most important linkages are between fishes and their echinoderm prey.

A number of studies have argued convincingly that populations of grazing sea urchins are strongly affected by the abundance of fish predators, particularly triggerfishes and pufferfishes. Such observations have been made in places as widespread as the Red Sea (Ormond et al. 1973; Messiha-Hanna & Ormond 1982), Kenya (McClanahan & Muthiga 1988), and the Caribbean (Hay 1984; Hay & Taylor 1985). Where urchin populations have expanded to high densities, a corresponding reduction in densities of fish predators by fishing has been documented.

In the Caribbean, the triggerfish *Balistes vetula*, a major predator of the urchin *Diadema antillarum*, is a favored food fish that is extremely vulnerable to trapping and spear-fishing (Clark et al. 1989; Roberts & Polunin 1991). Although triggerfish is rarely eaten in the Indo-Pacific, a reduction in its abundance there is probably also an effect of fishing because these species are frequently landed as by-catches. Removal of pufferfishes for the tourist trade has also been implicated in permitting increases in urchin abundance (Messa-Hanna & Ormond 1982). The most detailed evidence for the effects of fishing on urchin populations comes from the work of McClanahan and colleagues in Kenya. Fish densities and predation rates on urchins were four times greater on reefs protected from fishing than on unprotected reefs, and sea urchin densities were 100 times higher on unprotected reefs (McClanahan & Muthiga 1989; McClanahan & Shafir 1990).

Urchins have numerous and well-documented effects on reef communities, and changes in their abundance, both from epidemic disease and from removal of their predators, have resulted in marked effects on reef structure and processes. At high densities they reduce algal standing crop to very low levels (Sammarco 1982; Carpenter 1986; Levitan 1988), potentially competing with fish herbivores (Carpenter 1990; Robertson 1986; McClanahan 1992). They also exert a strong erosive effect

on the reef framework (Downing & El-Zahr 1987), reducing accretion rates and possibly leading to net erosion (McClanahan & Muthiga 1988). Figure 1a shows the probable relationship among reef benthic composition, fish predators of urchins, and urchins, and it shows how fishing could mediate a shift from one state to another.

In the Arabian region, Sheppard (1988) and Sheppard et al. (1992) have shown an uncoupling of reef growth from coral growth over gradients of increasing environmental stress. Although this is attributed to effects of the physical environment, it is also noteworthy that in the Arabian Gulf triggerfishes and pufferfishes disappear from reefs across these gradients (Roberts, unpublished data), and in their absence populations of urchins reach high levels (Downing & El-Zahr 1987), perhaps mediating the uncoupling of coral growth from carbonate accretion. In the Caribbean, increases in the carbonate accretion rate were recorded in some areas following the pathogenic mass mortality of the urchin *Diadema antillarum* in the early 1980s (Lessios 1988).

Recently it has been argued that loss of fish predators of juvenile crown-of-thorns starfish, due to fishing, has been responsible for outbreaks of the starfish on the Great Barrier Reef and elsewhere (Ormond et al. 1991). Although the evidence for this is far from certain, other explanations for the phenomenon are also unsatisfactory (Johnson 1992), and the idea merits further testing. Figure 1b shows this "predator control" model for crown-of-thorns starfish in graphical form, showing how fishing could mediate a shift from coral-dominated to algal-dominated reef communities. Possible losses of fish predators may also provide a key to the puzzling outbreaks of the corallivorous mollusc *Drupella* on Indo-Pacific reefs.

Loss of Top Predator Species

Fishing has caused massive reductions in the density of piscivorous fishes, such as groupers, on reefs throughout the tropics (Koslow et al. 1988; del Norte et al. 1989; Appeldoorn et al. 1992; Butler et al. 1993; Bohnsack et al. 1994). Despite this it is difficult to find evidence for any major effect of such losses on reef processes (Bohnsack 1982; Roberts & Polunin 1991; Bohnsack in press). In part this may be because such effects have not been investigated. It seems reasonable, however, that although linkages among fishes and their echinoderm prey have been striking, the effects of piscivore loss have gone unreported because their passing has little influence on the abundance of other species.

Pimm (1991) has made the case that systems in which species form a complex food web are more susceptible to cascades of species loss from removal of top predators than are simpler systems. Although reefs evidently fall into the category of complex systems, there is little support for this idea. Reefs are full of opportunistic

predators, and even apparent specialists may switch to feeding on the former prey of species removal by fishing (Randall 1967; Sano et al. 1984).

Good examples of dietary shifts followed the demise of the urchin *Diadema* in the Caribbean. The triggerfish *Balistes vetula* (Reinthal et al. 1984) and two species of toadfishes (Robertson 1987), previously specialist feeders on this urchin, shifted their diets toward a variety of invertebrate prey. In the case of toadfishes, where densities before and after *Diadema* mortality were measured, the urchin die-off had no effect on predator populations. Dietary flexibility among fishes probably goes a long way toward explaining the resilience of the reef ecosystem to the loss of top predators.

"Redundancy" in Reef-Fish Communities

Redundancy is a situation in which a number of species occupy a similar functional role within an ecosystem (Lawton & Brown 1993). If redundancy occurs in reef communities, then processes may not be compromised by the loss of a few species; thus, the effects of fishing are moderated. Many people feel very uncomfortable with the word redundancy when it is used in the context of species because it suggests that some species can be eliminated without adverse effects (Roberts 1994). Because our understanding of communities and ecosystems is still rudimentary, we clearly cannot accurately predict the effects of species loss. Nevertheless, the concept is useful and is probably made less contentious if cast in the form of "substitutability" of species.

There is ample evidence that reef communities are characterized by substantial substitutability of species. Sale (1974) was among the first to draw attention to the similar patterns of resource use among fish species. While his focus was upon damselfishes, it is clear that reefs contain many groups of functionally similar species (Hay 1994). Although all species differ in the details of their ecology, there is a relatively limited range of basic ways of making a living. Examples of functional groups include scraping herbivores, such as parrotfishes (and urchins); browsing herbivores, such as surgeonfishes and damselfishes; planktivores, such as fusiliers and damselfishes; and soft-substrate invertebrate feeders, including grunts and snappers.

Studies of feeding specialization among species within functional groups suggest that differences in diet may be determined by patterns of dominance and predation risk rather than by fixed characteristics of species (Robertson et al. 1979; Robertson 1984; Roberts 1985, 1987). For example, different species of planktivore tend to partition resources on the basis of size; larger species feed upstream of smaller and take bigger prey. Smaller fishes are able to gain access to these prey when the larger ones are removed (Coates 1980). Hence, loss of species from the reef system may have little overall ef-

fect on rates of planktivory or herbivory where there are similar species available to take over these roles.

Functional Redundancy and the Effects of Fishing

Based on present understanding, it appears that the role of piscivores in the reef community can be filled by other species. For many ecosystem processes, a single or a few species could probably fulfill the necessary role on their own, providing that reductions in density or biomass of other similar species were compensated by increases in theirs. For example, reef calcification rates are similar between reefs of the Australian Great Barrier Reef and the Eastern Pacific, despite an order of magnitude difference in the number of coral genera between regions (Glynn, unpublished data). Prior to the El Niño mass mortality of eastern Pacific corals (Glynn 1990), total levels of coral cover were similar between regions (Done 1982; Glynn & Wellington 1983). In some cases, however, functional redundancy may provide a scant buffer for the effects of intensive fishing. Reef fisheries typically employ nonselective methods capable of capturing a broad array of species, often characterized by similar morphology and behavior (Appeldoorn & Lindeman 1985; Russ 1991; Medley et al. 1993; Dalzell in press). Consequently, removal or population depletion of functionally similar species may occur, either simultaneously or sequentially, leading to loss of function. The example of fish predators of urchins has already been mentioned. Although there are usually several species that prey on urchins in any given region, all tend to be easily caught using the same fishing techniques (Roberts & Polunin 1991; Dalzell in press).

Also, populations may be depleted not only by direct capture but of by incidental effects of fishing. Russ and Alcala (1989) showed that populations of planktivorous fishes were greatly reduced in the Sumilon Island reserve following the breakdown of protection from fishing. Fusiliers, significant consumers of plankton, were important and were easily caught by fishermen. However, Russ and Alcala (1989) also documented a drop in populations of plankton feeding damselfishes, which they attributed to the use of habitat-destructive fishing techniques.

Does the loss of an entire functional group matter to reef processes? In some cases perhaps not, but in most it probably does. Continuing with the example of plankton feeders, current views suggest that planktivory forms an important route by which scarce nutrients can be "fixed" into the reef system (Hamner et al. 1988). How important such a loss is remains to be quantified, but the loss of planktivorous species could have widespread effects if this linkage proves significant.

Ultimate Effects of Sustained, Heavy Fishing

We are causing a massive, long-term perturbation of reef-community structure by fishing. As the world's pop-

ulation grows and fishing intensifies, the degree of modification exerted will increase. There is sufficient evidence to suggest that, over the long term, intense fishing will lead to major shifts in community and ecosystem structure (Done et al. in press) and that there will be substantial reductions in diversity, loss of physical complexity, loss of productivity, and loss of resilience of the reef system to other kinds of perturbation (Grigg 1994; Hughes 1994; Jennings & Lock in press; Polunin & Roberts 1993).

A glimpse of the future can be obtained by considering the role of fishing in phase shifts of reef communities from coral/invertebrate-dominated to algal-dominated (Done 1992). Moderate to high levels of grazing, by fishes or invertebrates, favor coralline algae over filamentous species (Steneck 1988). Coralline algae are important in reef accretion and in the stabilization of substrates (Vine 1974). Heavy fishing targets herbivorous as well as carnivorous species, removing all but the smallest individuals. The absence of urchin grazers, as in the Caribbean following the mass mortality of *Diadema antillarum* (Lessios 1988), may lead to dominance of reefs by filamentous and fleshy algae (Fig. 1a). Not only does this reduce calcification by coralline species, but it can lead to coral mortality and failure of recruitment (Ogden & Lobel 1978; Hughes et al. 1987). Such a phase shift has been documented in Jamaica (Hughes 1993, 1994) and elsewhere (Done 1992). If grazing pressure remains low, net erosion of the reef framework by bioeroders may ensue (Head & Hendry 1985).

Although I have focused on fishing, fishing does not occur in isolation. It may interact with other agents of disturbance, such as storms (Hughes 1993, 1994) or eutrophication (Head & Hendry 1985; LaPointe 1989), to exacerbate their effects and reduce the capacity of reefs to recover from them. We have ample information to demonstrate that fishing is a potent force of change on coral reefs, but we understand its effects insufficiently to predict exactly how reefs will respond to different intensities of fishing over the long-term. Fisheries organizations have generally done a good job of studying the effects of fishing at the population level. There is now an urgent need to extend research to higher levels of organization. Much can be learned from comparative studies across fishing gradients. Experimental approaches, however, ranging from small to large scales, will greatly enhance our understanding.

Experimental approaches are presently being initiated throughout the tropics, usually manipulating fishing effort or gear used. An approach rapidly gaining popularity is to study the effects of closing off areas to fishing (Plan Development Team 1990; Roberts & Polunin 1991, 1993; Dugan & Davis 1993; Bohnsack 1994, 1995). Although the proponents of these research initiatives have so far been fishery scientists or fish ecologists, it is essential that researchers from other disciplines become

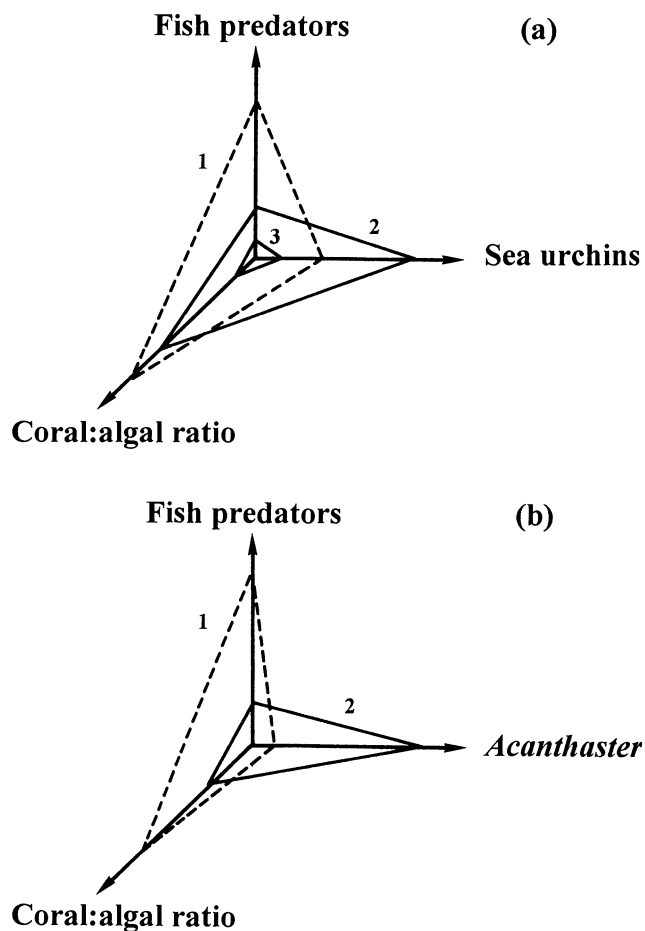


Figure 1. Phase diagrams showing possible linkages among reef benthic composition, fish predators, and their prey. The three axes indicate the abundance of fish predators of sea urchins, the abundance of sea urchins, and the ratio of coral to algal cover on the reef (a), and they indicate abundance of fish predators of the crown-of-thorns starfish (*Acanthaster planci*), starfish abundance, and the ratio of coral to algal cover on the reef (b). Part (a) shows how fishing can reduce numbers of urchin predators, resulting in increases in urchin populations and decreases in coral cover: unfished or lightly fished state (1), moderately fished state after depletion of urchin predators by fishing (2), and heavily fished state combined with pathogenic mass mortality of urchins in the Caribbean (3). Part (b) shows the proposed link between fish predators and crown-of-thorns starfish outbreaks and the resulting indirect effects of fishing on reef benthic composition: unfished or lightly-fished state (1), and fished state (loss of crown-of-thorns predators) leading to an outbreak of the coral-feeding starfish and a subsequent shift from coral to algal dominance (2). Figures are used with the permission of Jeremy Jackson and are adapted from Jackson (1994).

involved to help unravel the linkages among fishes and other reef components and processes, and so to determine with greater certainty how reefs respond to the changes wrought by humanity.

Conclusions

The appalling rate of tropical rainforest destruction has captured public concern in a way the destruction of reefs has failed to do. Yet the crisis of habitat and biodiversity loss is probably no less acute for the most diverse ecosystem in the sea than for that on land. Just as wholesale destruction of rainforests for timber and ephemeral agriculture has been criticized as a terrible waste of biological riches, so extractive fisheries on reefs may be a poor way of using these resources.

Birkeland has argued for a new paradigm upon which to base our attitudes toward diverse ecosystems (Birkeland, unpublished data). Coral reefs and rainforests are very productive, but this productivity is based on efficient recycling of nutrients; net production is actually very low. They are thus not well suited to large-scale extractive exploitation. Birkeland reasons that it would be better to concentrate harvests on systems with net nutrient inputs, such as upwelling regions, rather than on systems in which production and consumption are so closely balanced. We should perhaps view reefs and rainforests as libraries of genetic variation and sources of natural products that are capable of supporting low-level harvests only. This view may make good ecological sense, but it will not be easy to reduce the dependence of poor fishing communities on reefs and to stop them from harvesting them so intensively. By virtue of their complexity, reef fisheries are the most difficult in the world to manage. Nevertheless, a clearer understanding of the effects of fishing will at least give us a chance to manage reefs better and to provide a sustainable future for reefs and people alike.

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